

EXPERIMENTAL STUDIES ON THE GROWTH AND DEVELOPMENT OF STRAWBERRY PLANTS

BY
GEORGE M. DARROW

DISSERTATION SUBMITTED TO THE BOARD OF UNIVERSITY
STUDIES OF THE JOHNS HOPKINS UNIVERSITY IN
CONFORMITY WITH THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR
OF PHILOSOPHY

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BALTIMORE, MD.

Botanical Contribution from the Johns Hopkins University, No. 93.

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EXPERIMENTAL STUDIES ON THE GROWTH AND DEVELOPMENT OF STRAWBERRY PLANTS¹

By GEORGE M. DARROW²

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INTRODUCTION

The work reported in this paper constitutes a field study of the behavior of several varieties of strawberry plants during the greater part of the growing seasons of 1925 and 1926 at Glenn Dale, Md. Its purpose was to determine the environmental conditions most effective in promoting and limiting plant growth and development under field conditions. The general plan of the studies included detailed measurements of the plants growing in the field, especially of their leaf enlargement, in order to obtain numerical indices of their growth activity throughout the season, together with corresponding records of some of the main influential climatic conditions. The plant data were then compared with the climatic data to find out what correlations existed for the periods studied. The strawberry seems to be particularly adapted to studies on plant activity, because it is usually active from the opening of spring until the arrival of freezing weather, it is easily propagated vegetatively, and it is very tolerant of a wide range of climatic and soil conditions, although it responds with characteristic definiteness and promptness to slight climatic fluctuations. The results of the study show what conditions were most influential in the growth of the strawberry and present a general picture of its development throughout the growing season under Maryland conditions.

CLIMATIC RECORDS

The field records were taken at the United States Plant Field Station at Bell (post office Glenn Dale), Md. The work was begun in 1923 and continued through 1924, 1925, and 1926. As the principal records discussed herein are those of 1925 and 1926, climatic data for these years only are presented. Strawberries are commonly planted at the Bell station about April 1, and top growth usually ceases between October 15 and November 1. The growing season for tops therefore covers 6½ to 7 months, or about 210 days.

Air-and-soil thermograph records, records of white and black spherical porous porcelain atmometers, and records of soil-moisture content were taken in the field near the plants. Additional records were obtained from an official observation station of the United States Weather Bureau located but a few hundred feet from the strawberry field, and sunshine records were obtained from the weather station in Washington, D. C., about 15 miles distant.

¹ Received for publication Feb. 10, 1930; issued September, 1930.

² Thanks are due Prof. B. E. Livingston, director of the laboratory of plant physiology of the Johns Hopkins University, for assistance in planning and conducting the experiments.

The atmometers were placed in the plant rows with the spheres from 6 to 10 inches above the ground and somewhat above the foliage. Readings were taken daily or at longer intervals at about 7.30 a. m.

Records of the soil-moisture content were obtained from April to July, 1925, for the most part weekly.³ Cores were taken in duplicate in each of two spots about 100 feet apart in the plant rows. Each core was divided into three parts to represent three different ranges in depth, 1 to 6 inches, 6 to 12 inches, and 12 to 24 inches. The upper 6 inches had the lowest and the second foot the highest average moisture content for the period for which the records were taken. A marked decrease in moisture content occurred early in June at the period of high temperatures, high evaporation, and high transpiration rates. At no other time was the moisture supply very low, however, and it is not probable that the soil moisture supply at the Bell station was often a limiting factor in the early development of these plants. The moisture content for the upper 6 inches was used for these records.

The sunshine records for the two years correspond closely with the radiation indices, but show minor differences.

PLANT RECORDS

In 1925 nine varieties—Howard 17, Klondike, Missionary, Dunlap, Parsons, New York, Aroma, Sample, and Gandy—were used in the experiments. These include the leading commercially grown varieties, which constitute over 80 per cent of the total strawberry acreage in the United States. Two varieties, Howard 17 and Klondike, were more thoroughly studied than the others, being taken as representative of the northern and of the southern sorts, respectively. In 1926 these two varieties were the only ones used in the studies.

In 1925, 100 plants of each variety were selected for uniformity in size and general appearance and according to the dates when they rooted in 1924. On April 1 they were set in adjoining rows, and after becoming established the 10 plants of each variety at one end of each row were chosen for special study as representative of the 100 of each sort. Conditions were very favorable for the growth of these plants in 1925, and all made satisfactory development.

In the spring of 1926, 100-plant rows of Howard 17 and Klondike were set and a group of 12 plants near the north end of each row was selected for study. Growth was satisfactory but not as rapid in the early part of the season as in 1925.

The plan to obtain plant records at intervals of one week throughout each of the two seasons was generally followed, although some of the intervals were modified in both seasons. At each observation each new leaf that had expanded until most of its upper surface was exposed was numbered and tagged. Likewise, each new runner was numbered and tagged, or removed if that was required by the plan. All leaves and runners were then measured and recorded. The plant records, therefore, showed the complete history of each leaf and runner, including the leaves that developed at the tip of each runner. As runner tips became ready to take root they were pegged down in

³ The soil-moisture determinations were made by J. W. McLane, assistant biophysicist, Biophysical Laboratory, Bureau of Plant Industry.

position for rooting. In both 1925 and 1926 some of the selected plants were used for a study of their behavior after runners were removed. For this purpose, beginning June 17, 18, or 19 for different plants and continuing to the end of the growing season of 1925, all runners were removed from 5 of the 10 plants of each variety. In 1926 the runners were removed from 10 of the 12 plants, only 2 being allowed to form clons.

The records included leaf measurements, runner measurements, and records of the position of runners. The length and breadth of each of the three leaflets of each leaf and the length of each runner were obtained with a flexible centimeter rule. The length and the breadth were multiplied together to give the leaf product for each leaflet, and the products for the three leaflets were summed to give the leaf product for each leaf. The sum of the leaf product of all leaves gave the leaf product in square centimeters for the entire plant, which is used as an index (I) of its leaf area. To obtain the leaf-product increment for the interval the leaf product at the beginning of an interval was subtracted from that obtained at the end. The mean daily increment in leaf product for an interval was obtained by dividing the leaf-product increment for the interval by the number of days in the interval. Finally, the mean daily percentage increment in leaf product for a period was calculated in two ways, as follows: (1) By dividing the mean daily increment for the interval by the leaf product obtained at the beginning of the interval and multiplying by 100 to give index I_1 ; (2) by dividing the mean daily increment for the interval by the mean leaf product for the interval and multiplying by 100 to give index I_2 . Although the plants grew vigorously, as shown by their indices of leaf area (I) their mean daily increment and the indices I_1 and I_2 are relatively small.

In these studies the mean daily percentage increment in leaf product for any interval (I_2) is taken as an index of plant activity for that interval. The value of this index changes throughout the season, and its fluctuations are very nearly the same as the fluctuations in the rate of production of leaf surface and in the capacity of the plant to produce food. Leaf production is one of the main forms of activity in strawberry plants and may be considered as an index of general activity or growth.

Some special tests were made to determine the relation between these leaf-product values and actual leaf areas. Actual leaf area (by planimeter measurements) and leaf products were obtained for the same leaves of the Howard 17 variety. The results showed that actual leaf area was about 75 per cent of the corresponding leaf-product value with very slight variation. The leaf-product value for the entire leaf was much more satisfactory than was that for the terminal or for either of the lateral leaflets, and the leaf-product value for the terminal was more satisfactory than that of either lateral leaflet or that of the two laterals taken together. It was also found that the leaf product used in the tests was very much more satisfactory than any linear dimension, such as length of the leaflets.

The three indices (I , I_1 , and I_2) for each variety and interval from April 1 until June 9 are set forth in Table 1.

TABLE 1.—*Leaf-product indices (I , I_1 , and I_2) for nine strawberry varieties, 10 plants of each, by intervals from beginning of the growing season until about the beginning of runner formation, 1925*

Variety	Kind of index	Indices for interval No.—							
		0	1	2	3	4	5	6	7, 8
		Apr. 1-14	Apr. 15-21	Apr. 22-28	Apr. 29-May 5	May 6-12	May 13-20	May 21-26	May 27-June 9
Howard 17	I	53	91	134	168	235	397	578	1,091
	I_1		10.2	6.7	4.6	5.7	8.7	7.6	6.3
	I_2		7.5	5.4	4.0	4.7	6.5	6.4	4.4
Missionary	I	21	44	81	105	166	278		^a 874
	I_1		15.7	12.0	4.2	8.3	9.0		^a 10.2
	I_2		10.0	8.4	3.7	6.4	6.3		^a 5.2
Dunlap	I	18	33	54	68	96	^b 160		501
	I_1		11.7	9.1	3.7	5.9	^b 9.5		^c 9.7
	I_2		8.1	6.8	3.3	4.9	^b 7.1		^c 4.7
New York	I	27	45	73	97	159	258		^c 800
	I_1		9.6	8.9	4.7	9.2	8.9		^c 9.5
	I_2		7.1	6.8	4.0	6.9	7.1		^c 4.7
Aroma	I	19	34	57	72	115	162		^d 415
	I_1		11.1	9.7	3.7	8.5	5.8		^d 6.8
	I_2		8.1	7.1	3.3	6.5	4.9		^d 3.8
Gandy	I	19	35	59	79	106	187	^e 446	589
	I_1		12.1	9.7	4.9	4.9	10.9	^e 9.7	3.6
	I_2		8.5	7.3	4.2	4.2	7.9	^e 5.8	3.1
Average of 6 varieties	I		11.7	9.4					
	I_1		8.2	7.0					
	I_2								
Klondike	I	37	60	107	144	219	342	493	986
	I_1		8.9	11.2	4.9	7.4	7.0	7.4	7.1
	I_2		6.7	8.0	4.2	5.9	5.4	6.0	4.8
Parsons	I	24	34	59	81	136	227		^c 728
	I_1		5.8	10.6	5.3	9.8	9.6		^c 10.0
	I_2		4.9	7.6	4.5	7.2	7.1		^a 4.8
Sample	I	28	50	96	118	172	243	^e 468	^f 749
	I_1		11.1	13.2	3.2	6.5	5.9	^e 6.5	^f 6.7
	I_2		8.1	9.0	2.9	5.3	4.9	^e 4.5	^f 5.1
Average of 3 varieties	I		8.6	11.7					
	I_1		6.6	8.2					
	I_2								
Average of 9 varieties	I				4.4	7.4	8.4	8.5	8.3
	I_1				3.8	5.8	6.2	5.7	4.9
	I_2								

^a For interval May 21 to June 9.^b For interval May 13 to 19.^c For interval May 20 to June 10.^d For interval May 20 to June 11.^e For interval May 20 to June 2.^f For interval June 3 to June 11.

At the end of the last interval shown in Table 1 (ending June 9, 1925), the 10 plants of each variety were divided into two groups of five plants each and all runners were removed from the plants of one group as they were produced. Measurements were discontinued at different times for the different varieties as shown in Table 2.

TABLE 2.—*Leaf-product indices (I, I₁, and I₂) for nine strawberry varieties, five plants of each with runners left on and five plants of each with runners removed, by intervals from about the beginning of runner formation until the end of observations, 1925*

Variety and group	Kind of index	Indices for interval No.—									
		9	10	11	12	13	14	15	16	17	18
		June 10-16	June 17-23	June 24-30	July 1-7	July 8-14	July 15-22	July 23-28	July 29-Aug. 6	Aug. 7-19	Aug. 20-Sept. 16
<i>Howard 17</i>											
With runners.....	<i>I</i>	^a 1,346	1,772	2,323	2,885	3,541	4,035	4,781	7,043	10,669	^b 16,551
	<i>I</i> ₁	^a 3.2	4.8	4.4	3.5	3.2	1.8	3.1	5.3	4.0	^b 2.1
	<i>I</i> ₂	^a 2.2	4.1	3.8	3.1	2.9	1.7	2.8	4.3	3.1	^b 1.6
Without runners.....	<i>I</i>	-----	1,388	1,623	1,879	2,138	2,184	2,375	2,704	2,886	^b 4,590
	<i>I</i> ₁	-----	1.6	2.6	2.3	2.0	.3	1.4	1.7	0.5	^b 0.7
	<i>I</i> ₂	-----	1.5	2.2	2.1	1.8	.3	1.3	1.4	.5	^b .7
<i>Klondike</i>											
With runners.....	<i>I</i>	1,389	1,772	2,409	2,963	3,682	^c 4,566	^d 5,890	-----	^e 16,762	^b 2,427
	<i>I</i> ₁	3.5	4.0	5.1	3.3	3.5	^c 2.6	^d 4.8	-----	^e 6.8	^f 2.1
	<i>I</i> ₂	3.1	3.5	4.4	2.9	3.1	^c 2.4	^d 4.2	-----	^e 3.6	^f 1.2
Without runners.....	<i>I</i>	959	1,130	1,362	1,606	1,786	^c 2,097	^d 2,244	-----	^e 2,809	^f 1,775
	<i>I</i> ₁	1.7	2.5	2.9	2.6	1.6	^c 1.9	^d 1.2	-----	^e 1.0	^e -0.5
	<i>I</i> ₂	1.6	2.3	2.7	2.3	1.5	^c 1.8	^d 1.0	-----	^e .8	^e -.6
<i>Missionary</i>											
With runners.....	<i>I</i>	1,095	1,434	1,909	^c 3,253	-----	-----	-----	-----	-----	-----
	<i>I</i> ₁	4.7	4.4	4.7	^c 4.4	-----	-----	-----	-----	-----	-----
	<i>I</i> ₂	4.1	3.8	4.1	^c 3.3	-----	-----	-----	-----	-----	-----
Without runners.....	<i>I</i>	209	966	1,221	^c 1,682	-----	-----	-----	-----	-----	-----
	<i>I</i> ₁	2.3	2.8	3.8	^c 2.4	-----	-----	-----	-----	-----	-----
	<i>I</i> ₂	2.1	2.5	3.3	^c 2.0	-----	-----	-----	-----	-----	-----
<i>Dunlap</i>											
With runners.....	<i>I</i>	^h 511	ⁱ 777	1,010	ⁱ 1,916	-----	-----	-----	-----	-----	-----
	<i>I</i> ₁	^h 3.7	ⁱ 4.5	4.3	ⁱ 5.6	-----	-----	-----	-----	-----	-----
	<i>I</i> ₂	^h 3.3	ⁱ 4.0	3.7	ⁱ 3.9	-----	-----	-----	-----	-----	-----
Without runners.....	<i>I</i>	^h 574	ⁱ 670	827	ⁱ 1,194	-----	-----	-----	-----	-----	-----
	<i>I</i> ₁	^h 2.9	ⁱ 2.8	3.4	ⁱ 2.8	-----	-----	-----	-----	-----	-----
	<i>I</i> ₂	^h 2.7	ⁱ 2.6	4.0	ⁱ 2.5	-----	-----	-----	-----	-----	-----
<i>Parsons</i>											
With runners.....	<i>I</i>	^h 842	ⁱ 1,087	1,528	-----	-----	-----	-----	-----	-----	-----
	<i>I</i> ₁	^h 5.2	ⁱ 4.8	5.8	-----	-----	-----	-----	-----	-----	-----
	<i>I</i> ₂	^h 4.4	ⁱ 4.2	4.8	-----	-----	-----	-----	-----	-----	-----
Without runners.....	<i>I</i>	^h 853	ⁱ 1,068	ⁱ 1,194	-----	-----	-----	-----	-----	-----	-----
	<i>I</i> ₁	^h 1.7	ⁱ 4.2	3.2	-----	-----	-----	-----	-----	-----	-----
	<i>I</i> ₂	^h 1.6	ⁱ 3.7	2.9	-----	-----	-----	-----	-----	-----	-----
<i>New York</i>											
With runners.....	<i>I</i>	ⁱ 917	^k 1,107	ⁱ 1,438	-----	^m 2,567	-----	-----	-----	-----	-----
	<i>I</i> ₁	ⁱ 4.2	^k 4.1	ⁱ 3.7	-----	^m 3.2	-----	-----	-----	-----	-----
	<i>I</i> ₂	ⁱ 3.6	^k 3.7	ⁱ 3.3	-----	^m 2.4	-----	-----	-----	-----	-----
Without runners.....	<i>I</i>	ⁱ 1,075	^k 1,293	ⁱ 1,452	-----	^m 2,823	-----	-----	-----	-----	-----
	<i>I</i> ₁	ⁱ 2.7	^k 4.1	ⁱ 1.5	-----	^m 2.0	-----	-----	-----	-----	-----
	<i>I</i> ₂	ⁱ 2.4	^k 3.7	ⁱ 1.4	-----	^m 1.2	-----	-----	-----	-----	-----
<i>Aroma</i>											
With runners.....	<i>I</i>	ⁿ 518	-----	-----	-----	-----	-----	-----	-----	-----	-----
	<i>I</i> ₁	ⁿ 4.1	-----	-----	-----	-----	-----	-----	-----	-----	-----
	<i>I</i> ₂	ⁿ 3.6	-----	-----	-----	-----	-----	-----	-----	-----	-----
Without runners.....	<i>I</i>	ⁿ 441	-----	-----	-----	-----	-----	-----	-----	-----	-----
	<i>I</i> ₁	ⁿ 4.4	-----	-----	-----	-----	-----	-----	-----	-----	-----
	<i>I</i> ₂	ⁿ 3.8	-----	-----	-----	-----	-----	-----	-----	-----	-----

^a Indices for all 10 plants.^b Average of 2 plants instead of 5 plants.^c For interval July 15 to 23.^d For interval July 24 to 30.^e For interval July 31 to Aug. 26.^f For interval Aug. 27 to Sept. 18 and average of 2 plants instead of 5 plants.

For interval July 1 to 16.

^h For interval June 11 to 17.ⁱ For interval June 18 to 23.^j For interval June 11 to 18.^k For interval June 19 to 23.^l For interval June 24 to July 1.^m For interval July 2 to 23.ⁿ For interval June 12 to 18.

TABLE 2.—*Leaf-product indices (I , I_1 , and I_2) for nine strawberry varieties, five plants of each with runners left on and five plants of each with runners removed, by intervals from about the beginning of runner formation until the end of observations, 1925—Continued*

Variety and group	Kind of index	Indices for interval No.—									
		9	10	11	12	13	14	15	16	17	18
		June 10-16	June 17-23	June 24-30	July 1-7	July 8-14	July 15-22	July 23-28	July 29-Aug. 6	Aug. 7-19	Aug. 20-Sept. 16
<i>Sample</i>											
With runners.....	I	ⁿ 982									
	I_1	ⁿ 4.6									
	I_2	ⁿ 4.0									
Without runners.....	I	ⁿ 762									
	I_1	ⁿ 2.1									
	I_2	ⁿ 1.9									
<i>Gandy</i>											
With runners.....	I	ⁿ 741									
	I_1	ⁿ 3.3									
	I_2	ⁿ 2.9									
Without runners.....	I	ⁿ 787									
	I_1	ⁿ 3.8									
	I_2	ⁿ 3.4									
<i>Average of all varieties</i>											
With runners.....	I_1	4.4	4.4	4.7	3.4	3.4	2.2	4.0	5.4	5.3	2.5
	I_2	3.7	3.6	4.0	3.0	3.0	2.1	3.5	4.7	3.3	1.6
Without runners.....	I_1	3.1	2.9	2.9	2.5	1.8	1.2	1.3	1.4	.8	.2
	I_2	2.6	2.7	2.6	2.0	1.6	1.1	1.2	1.2	.7	.1

^a For interval June 12 to 18.

In 1926 the period of observations extended from June 26 to October 9. The index values obtained are shown in Table 3. Two series of values are shown for each variety, one for the 2 plants with runners (these becoming clons) and the other for the 10 plants without runners.

TABLE 3.—*Leaf-product indices (I , I_1 , and I_2) for two strawberry varieties, 2 plants of each with runners left and 10 of each with runners removed, by intervals from about the beginning of the season of runner formation until about the end of the growing season, 1926*

Variety and group		Kind of index	Indices for interval No.—											
			1	2	3	4	5	6	7	8	9	10	11	12
			June 26- July 6	July 7-12	July 13-19	July 20-26	July 27- Aug. 2	Aug. 3-9	Aug. 10- 16	Aug. 17- 23	Aug. 24- 30	Aug. 31- Sept. 7	Sept. 8-21	Sept. 22 to Oct. 7-9
<i>Howard 17</i>														
With runners.....	<i>I</i>	871	1,269	1,526	1,905	2,610	2,899	2,618	3,419	3,934	5,099	8,433	12,954	
	<i>I</i> ₁	4.7	6.5	2.9	3.5	5.3	1.6	-0.6	3.2	2.2	5.3	4.0	3.3	
	<i>I</i> ₂	3.7	5.3	2.6	3.2	4.5	1.5	-1.6	2.7	2.0	4.6	3.1	2.6	
Without runners.....	<i>I</i>	738	1,014	1,108	1,307	1,560	1,673	1,348	1,581	1,586	1,897	2,148	2,655	
	<i>I</i> ₁	4.3	8.9	1.3	2.4	2.7	1.0	-2.8	2.5	0	2.3	0.9	1.5	
	<i>I</i> ₂	3.5	7.8	1.3	2.2	2.5	1.0	-3.1	2.3	0	2.1	.9	1.3	
<i>Klondike</i>														
With runners.....	<i>I</i>	812	849	1,168	1,287	1,604	1,604		^a 2,124	2,518	3,308	4,452	5,614	
	<i>I</i> ₁	3.9	0.7	5.4	1.5	4.2	-0.5		^a 2.3	2.6	3.9	2.5	1.4	
	<i>I</i> ₂	3.2	.6	4.2	1.4	3.7	-.5		^a 2.0	2.4	3.4	2.1	1.2	
Without runners.....	<i>I</i>	410	456	635	758	859	845		^a 788	565	864	940	1,022	
	<i>I</i> ₁	5.3	1.9	5.6	2.8	1.9	-0.2		^a -0.5	-4.0	6.6	0.6	0.5	
	<i>I</i> ₂	4.1	1.8	4.7	2.5	1.8	-2		^a -0.5	-4.7	5.2	.6	.5	
<i>Average</i>														
With runners.....	<i>I</i> ₁	4.3	3.6	4.2	2.5	4.8	.6		2.8	2.4	4.6	3.3	2.4	
	<i>I</i> ₂	3.5	3.0	3.4	2.3	4.1	.5		2.4	2.2	4.0	2.6	1.9	
	<i>I</i>	4.8	5.4	3.5	2.6	2.3	.4		.7	-2.0	4.5	.8	1.0	
Without runners.....	<i>I</i> ₂	3.8	4.8	3.0	2.4	2.2	.4		.6	-2.4	3.7	.8	.9	

^a For interval Aug. 10 to 23.

When the intervals in Tables 1, 2, and 3 were the same for all varieties considered, the average index values were derived in the ordinary manner; when the intervals differed so that the averages could not be obtained in the ordinary way, those for the actual intervals used were first plotted as ordinates on a graph with these intervals as abscissas, and the average values were read from the graph for the dates required.

Because the varieties Klondike, Parsons, and Sample behaved differently from the remaining six for the first two intervals of 1925 (Table 1), the averages for these intervals were determined for these three varieties and for the remaining six separately. The two groups behaved similarly throughout the summer after the first two intervals, and for later intervals their index values were combined in single averages and taken to represent both groups together.

The data for climatic values and for leaf-product indices are presented in Figures 1 and 2. Figure 3 shows the appearance of a part of the experimental rows in 1926 with leaves tagged and runner plants pegged.

DISCUSSION

COMPARISON OF LEAF-PRODUCT AND CLIMATIC GRAPHS

A comparison of the plant graphs in the lower parts of Figures 1 and 2 with the climatic graphs in the upper parts of the same figures brings out the fact that the two sets of graphs are not generally in agreement for either season. The seasonal march of the leaf-product indices does not follow the march of any one of the climatic indices here used, but shows the influence of different climatic factors. The first two intervals of 1925 may be disregarded as being especially influenced by genetic differences. The second index (I_2) appears more useful than the first (I_1) and is used in the discussion.

The first elevation of the leaf-product graph for 1925 (intervals 4 to 7) corresponds to temperature, evaporation, radiation, and sunshine-duration values from low to medium, and to high soil-moisture values. The second elevation (interval 16) for the clons, corresponds to a definite depression in the temperature graph and to low values of evaporation, radiation, sunshine duration, and high soil-moisture content. The first elevation of the leaf-product graph for 1926 (interval 5) corresponds to a depression in the temperature-maximum graph, to an elevation in the temperature-minimum graph, and to relative depressions in the graphs for evaporation, radiation, and sunshine duration. The second elevation (interval 10) corresponds to medium values for temperature, evaporation, and radiation, and to a low value for sunshine duration.

The first depression of the graph for 1925 (interval 3) corresponds in time to exceptionally low values for all four temperature indices and to relatively low values for evaporation, radiation, and sunshine duration, but the soil-moisture content for this interval is high. The broad second depression for 1925 (intervals 9 to 15) corresponds to high temperature values throughout, to low or medium soil-moisture values, to high evaporation and radiation values, and to medium sunshine-duration values.

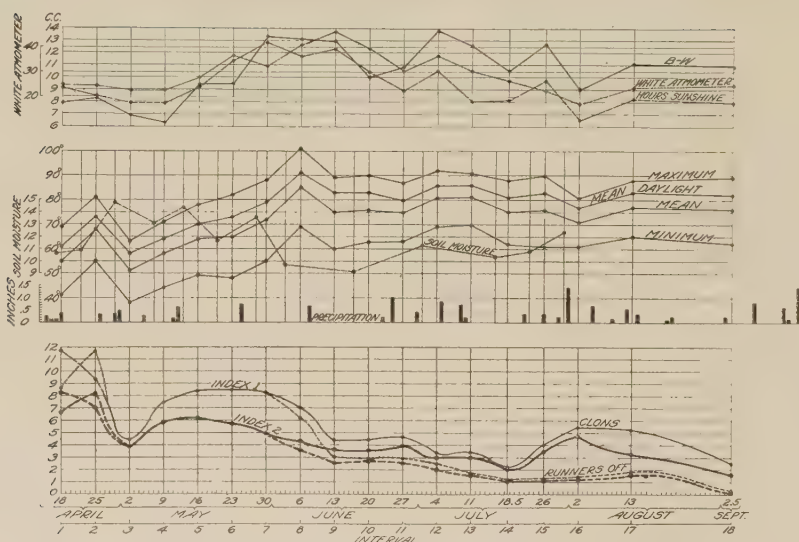


FIGURE 1.—Plant activity shown in terms of leaf-product indices (I_1 and I_2) of the strawberry for 1925 at the United States Plant Field Station, Bell, Md., together with temperature, rainfall, soil-moisture, evaporation, and sunshine graphs for the same period

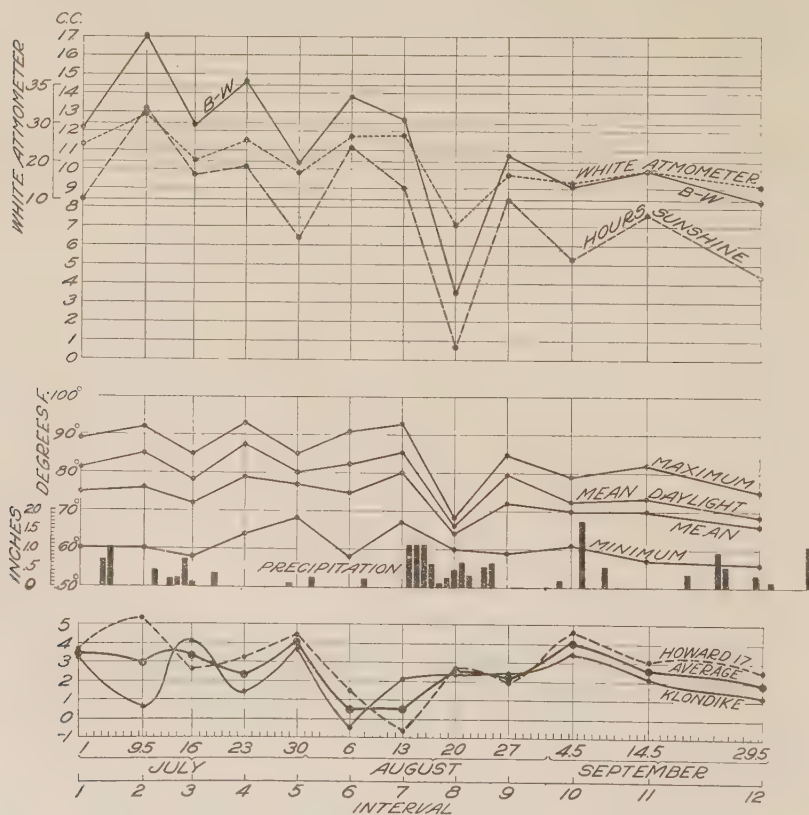


FIGURE 2.—Plant activity shown in terms of leaf-product indices (I_1) in Klondike and Howard 17 strawberry plants and of their average for 1926 with corresponding climatic data



FIGURE 3.—Strawberry plants, Howard 17 (at left) and Klondike (at right), on which growth studies were made in 1926. The plant of Howard 17 in the immediate foreground had all runners removed as fast as formed, while the next plant had its runners pegged to the soil in order to induce them to root promptly

The pronounced depression of the leaf-product graphs for 1926 does not correspond to any of the climatic graphs thus far considered, but it is to be remembered that there is no soil-moisture graph for this season. However, an examination of the precipitation graph shows that this depression of the leaf-product graph represents, in time, the end of a long drought period, and it is safe to suppose that the soil-moisture values at that time were very low.

Considering now only the plant graphs and those for average mean daylight temperature, some indications as to the air-temperature conditions that apparently have been especially favorable or unfavorable for rapid leaf production may be reached. In both seasons high leaf-product values occur for intervals with daylight-temperature values approximately between 64° and 80° F., and low leaf-product values occur for intervals with daylight-temperature values of about 79° or above, and also of 68° or below. These observations, together with many details shown on the graphs, lead to the conclusion that temperature was generally the limiting factor in the production of leaves on the plants used in these studies. In these two seasons the moisture conditions were probably generally adequate, with the exception noted for intervals 6 and 7 of 1926, and no specific influence can be postulated for the conditions of evaporation, radiation, and sunshine duration except in those cases where temperature influence was also indicated. It may therefore be supposed that there was a range of daylight-temperature values from about 64° to 80° within which leaf production went on at high rates, whereas daylight-

temperature values higher or lower than this range gave characteristically low rates of leaf production. It is to be noted that these limits are not exactly the same when derived from the occurrence of high leaf-product values as when derived from the occurrence of low leaf-product values. From these results it might be concluded that the optimum value for the daylight mean is not far from 73° (perhaps between 70° and 76°). This same optimum has been derived by studying these graphs in several other ways, and it may be taken tentatively as approximately correct for the data at hand.

Though plant activity as measured by the leaf-product method indicates low rates below 64° and above 80° F., it should be emphasized that this applies to the plants under the conditions of this study. The responses might be different with the long days in Alaska and the varieties grown there or under irrigation at high elevations in Western States. However, because the varieties included the leading sorts grown in the United States and because of the variety of climatic conditions encountered, it is probable that the activity of tops during most of the growing period responds in a similar manner to these temperatures in the humid regions of the United States. Strawberries are raised successfully in the South, where high temperatures are often encountered during the summer, because there some growth can take place from time to time throughout the long growing season and because of the occurrence of periods with temperatures near the optimum in fall and spring. In the North the strawberry succeeds because the temperatures are near the optimum during much of the summer, even though they are below the optimum during most of the spring and fall.

SEASONAL MARCH OF MATURE-LEAF SIZE AS INDICATED BY MEAN LEAF PRODUCT

The measurement at regular intervals of each leaf on all plants in these studies made it possible to obtain data showing how the leaf size of mature leaves was related to the time of year when they unfolded from the bud, and to their position, whether on parent or runner plants; also, how the production of runner plants influenced mature-leaf size in the mother plants. Four plants of the Howard 17 variety were used for this study. Two were of the group allowed to produce runners and to form clons, and the other two were of the group from which all runners were removed. The leaves were classed according to the dates on which they were first observed unfolding from the bud. After the beginning of runner-plant formation the data for the two plants with runners removed were separated from those for the two producing runner plants. In addition, the runner plants themselves were classed according to the dates on which they were first observed as plants. The data obtained from these leaf measurements were plotted to form the graphs shown in Figure 4.

It will be noted that the graph for mother plants rises at first slowly then rapidly until June 10, when runner plants began to be formed. (Fig. 4.) After June 24, the graph for mother plants with runners (producing runner plants) shows a decided drop, which continues, except for a slight rise July 8, until the end of the period. The graph for mother plants with runners removed maintains its high level, rising from July 1 to July 23. For the period from the

beginning of observation to the beginning of runner-plant formation the leaves of successive leaf classes were progressively larger when enlargement had ceased, that is, the later they unfolded from the bud the larger they became. When runners were removed as they formed, thus preventing the formation of runner plants and the presumable corresponding drain on the mother plant, the leaves of later leaf classes became even larger. But when runner plants were allowed to form, the period of runner-plant formation was characterized by smaller mature leaves on the mother plant. The greatest mean leaf product is for the leaf class of August 7, and its value is 160, which is more than four times as great as the corresponding mean for leaves of the first leaf class (April 15) which had passed the winter in the buds. For the mother plants that were

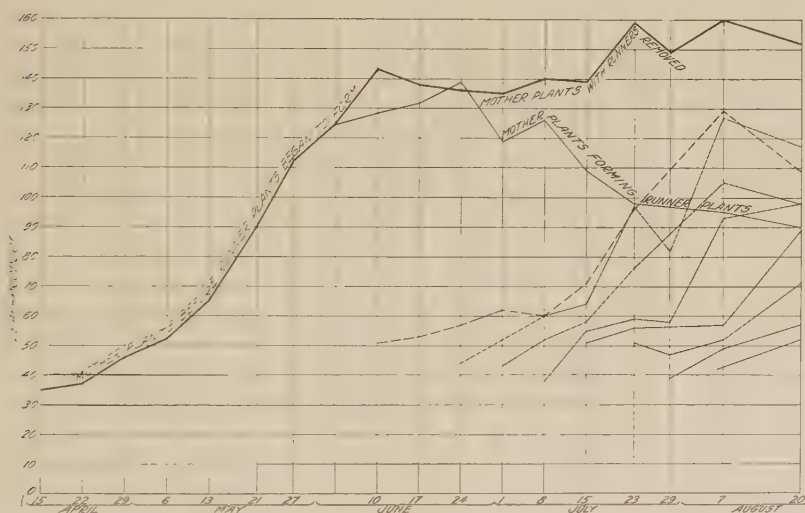


FIGURE 4.—Graph showing (for plants of Howard 17) average size of mature leaves (leaf product) for each leaf class: For mother plants before runner plants began to be formed (broad line before June 10); for mother plants with runners removed (broad line after June 10); and for mother plants forming runner plants (narrow line), as well as for runner plants of each runner-plant class (broken lines). Abscissas represent leaf classes (designated by date on which leaves unfolded from bud) and runner-plant classes (designated by date on which runner plants were formed); ordinates are the average leaf products

allowed to produce runner plants the leaves of the leaf class of August 7 gave a mean leaf product of only 95 when enlargement ceased. Thus, the removal of runners had increased the mean leaf product for this leaf class by more than 50 per cent.

Turning to the graphs (fig. 4) for mean leaf products of leaves on runner plants, it may be noted that the first leaf class in each runner-plant class gave a mean leaf product of the same general order of magnitude as that given by leaves of the first three or four leaf classes of the mother plants, and this seems to be true without reference to the runner-plant class. That is, the first leaves produced by a runner plant apparently attained about the same size when mature, whether the plant took root June 10 or August 7 or at any intervening time, and the size attained was practically the same as that reached by mother-plant leaves that unfolded at the beginning of the season.

This relation is especially striking when it is recalled that the environmental conditions of early spring differed greatly from those of mid-summer.

Furthermore, the graphs for successive runner-plant classes closely resemble in shape the graph for the parent plants before runner plants began to form. For any runner-plant class the graph slopes upward, at first slowly and then more rapidly. In the first three runner-plant classes (June 10 and 24 and July 1) a maximum in mature-leaf size is shown for the leaves of the leaf class of August 7, just as in the case of the leaves of the mother plants from which runners were removed. The actual maximum leaf products for the first two runner-plant classes (June 10 and 24) are much smaller (129 and 127) than the corresponding value for the plants with runners removed (160), but much greater than that for the mother plants producing runner plants (95). The maximum for the third runner-plant class (July 1) is smaller, but still greater than the mother-plant value just mentioned. The succeeding five runner-plant classes each gave progressively larger mature leaves with successive leaf classes, but apparently the growing season was not long enough to allow the graphs of these runner-plant classes to show maxima. At any rate, for these last five runner-plant classes, leaves of the leaf class of August 20 gave higher mean leaf products at maturity than did those of the leaf class of August 7.

It seems to be indicated that under the conditions of this test, with apparently ample moisture, the size of a runner-plant leaf at maturity was determined largely by the age of the runner plant at the time the leaf unfolded, rather than by the special environmental conditions prevailing either at the time the runner plant rooted, at the time the leaf unfolded, or during the period of enlargement of the leaf.

From the results of this study of mature-leaf size the following picture of some aspects of the development of the strawberry plants dealt with may be tentatively presented. The early developmental stages of the spring-set plant consist in a rapid enlargement of the leaf and root systems by which the rate of net income in all necessary materials is rapidly increased; enlargement of leaf and root systems and the general maintenance of health cost the plant a considerable quantity of essential materials, but the increased income more than offsets these costs from a very early period of development. A larger root system results in a more rapid supply of water and salts from the soil, and a larger leaf system results in a more rapid production of the products of photosynthesis. Leaves that unfold later are therefore better supplied with needed materials than are those that unfold earlier. The later ones should therefore approach the genetic maximum leaf size for the variety considered. But the production of runners and runner plants soon begins, and these are more active in growth than the crown of the parent plant, apparently actually decreasing its supply of necessary materials and limiting the enlargement of leaves that unfold from the crown after runner formation has set in. For a time the runner plant seems to hold the advantage, and its leaves become larger than those contemporaneously developed from the crown, thus approaching the maximum leaf size for the given variety. In its early stages of development the runner plant receives from the parent crown relatively large quantities of water, salts, and the products of photosynthesis. It soon forms, in addition, large

quantities of the products in its own rapidly enlarging leaf system, and derives additional water and salts through its own root system, especially since its roots enter regions of soil not previously explored by the roots of the parent plant.

In turn, the runners and runner plants produced by the first runner plants to be formed from a mother plant may indirectly affect the mother plant itself to some extent, and their relations to the first runner plants are in general the same as those that obtain between the original crown and the first runner plants.

LONGEVITY OF LEAVES AS RELATED TO TIME OF UNFOLDING

Although the strawberry is an evergreen plant, at the Bell station its individual leaves do not live even throughout the growing season. The first leaves to die are those that passed the winter in the expanded mature condition and the next are those that were partially developed in the preceding fall and passed the winter in the bud. Leaves produced entirely in the spring live longer than either overwintering kind.

To study the relative length of life of leaves that unfold at different times in the growing season, data derived from the five plants of the Howard 17 variety with runners removed were employed. The leaves were serially numbered, the length of life was determined for each leaf, and the resulting values were grouped by leaf classes and by length of life in each class. These data include 12 leaf classes from April 15 to July 8, 1925, for all five plants grouped together. Each class includes all leaves first observed as unfolded on the date representing their class. In any leaf class there was considerable variability in leaf longevity, but all leaves of each of the first seven classes (April 15 to May 27) were observed to have died by August 6. Some leaves in each of the later classes were still alive on August 10 when observations on time of death were discontinued.

The results obtained are presented in Figure 5. Approximate dates of unfolding and of death are shown as abscissas, and the serial numbers of the 118 leaves that were studied are shown as ordinates. The height of the shaded blocks at the left-hand end indicates the serial numbers of the leaves and consequently the total number in each leaf class. Each block is bounded at the right by a stepped line the vertical portions of which show the approximate dates of death of the corresponding leaves. The lowest serial leaf numbers in each class refer to the shortest lived leaves of the class. For example, 10 leaves were observed as unfolded on April 15, and these are serially numbered from 1 to 10; therefore the leaf class of April 15 included leaves Nos. 1 to 10. Eight of these (Nos. 1 to 8) were recorded as dead on June 10 and the remaining two (Nos. 9 and 10) on June 17. The second leaf class included six leaves (Nos. 11 to 16). Of these, one died June 10, three June 17, one June 24, and the remaining one July 1. The blocks for later leaf classes may be interpreted in a similar manner by reference to the marginal scales. Of the 118 leaves studied, 87 had died by August 19. Their length of life ranged from 21 to 77 days and averaged 56 days. It may therefore be said that the mean or normal longevity of these summer leaves was nearly two months.

In a general way the leaves died in sequence, those of the earlier classes dying first; but exceptions will be noted, doubtless owing to peculiar conditions operating in these cases. It is not possible to state

just why some leaves of a given class died before others of the same class. Leaf-spot diseases (caused by infection by *Macrospirella* or *Dendrophoma*) may have been a contributing factor, but general observation led to the conclusion that infection was not generally important in determining the dates of death of an infected leaf. Infection was not usually observed until the leaves were mature or past maturity. Old leaves may have offered exceptionally favorable conditions for infection. The appearance of these leaf spots almost exclusively on older leaves can hardly be related to a more or less fixed period necessary for the preliminary development of the fungus within the tissues, for other varieties susceptible to these diseases showed severe injury within a few days after the leaves unfolded.

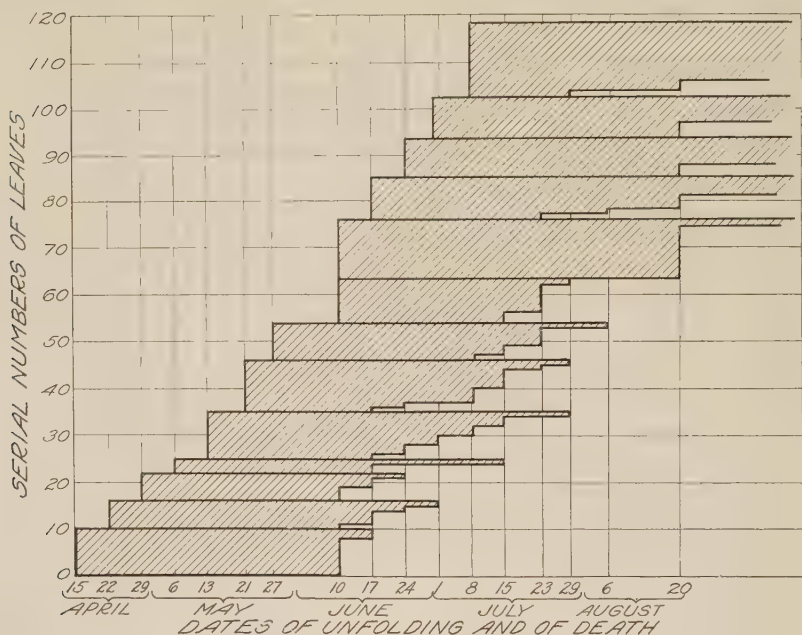


FIGURE 5.—Length of life of all leaves produced by five plants of the Howard 17 strawberry with runners removed, from April 1 to July 8, 1925

COMPARISON OF VARIETIES WITH RESPECT TO NET LEAF PRODUCTION

Seven different varieties were compared with respect to the seasonal march of the value of the average total leaf product per plant, and the results are shown graphically in Figure 6, the data for which are derived from Tables 1 and 2. Ten plants of each variety, together with their runner plants, were used in obtaining the average values. The scale of values of the average total leaf product per plant is shown at the left, and the progress of the season (from April 15 to July 1, 1925) is shown by points and dates along the base line.

For all varieties development is seen to have been slow until about May 13, after which net leaf production was more rapid. In general the relative position of the several lines remains the same throughout their course; varieties with larger values at the beginning of this period had larger values throughout, for there is little crossing of the

lines of the figures. The most active variety was Howard 17 and the least active was Aroma. The latter generally makes but poor growth on the sandy soil of Bell station.

COMPARISON OF NET LEAF PRODUCTION IN PLANTS WITH RUNNERS REMOVED
AND WITH RUNNERS LEFT ON AND ALLOWED TO ROOT

The seasonal march of the average value of the total leaf product per plant was studied for the period from April 15 to August 20, 1925,

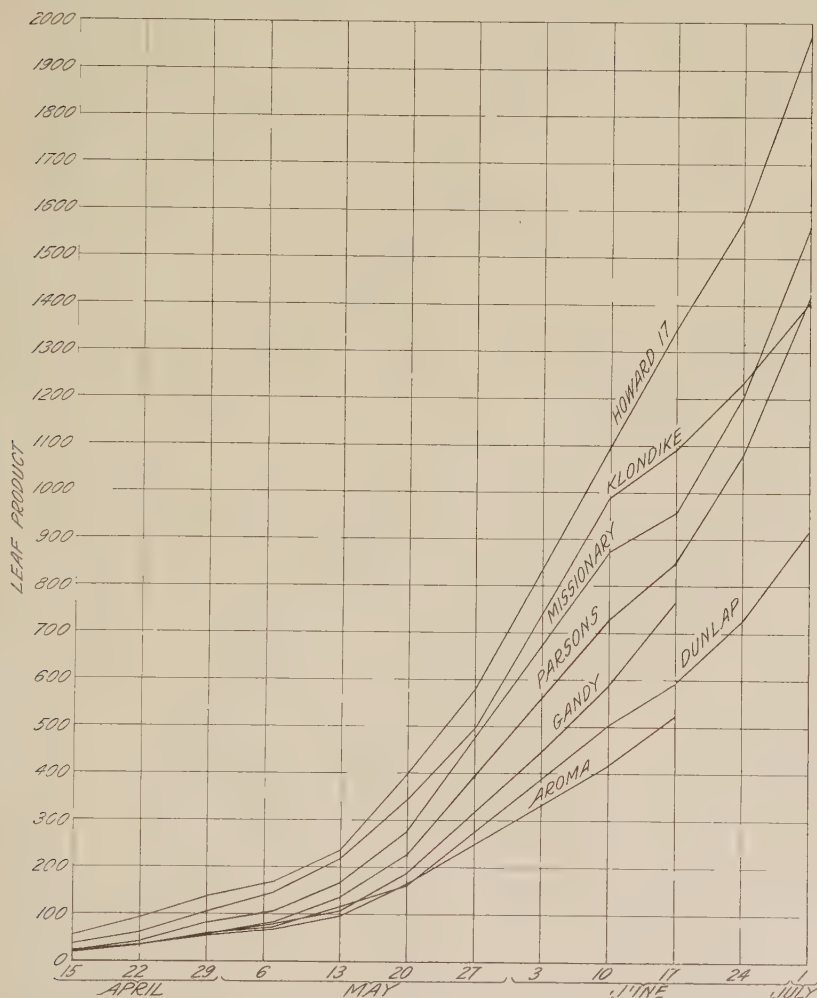


FIGURE 6.—Seasonal marches of total leaf area per plant (as indicated by average values of total leaf product per plant) for each of seven different varieties of strawberry. Ten plants with their runner plants were used for each variety, and all were set out April 1, 1925

for plants with runners removed and with runners left and allowed to produce runner plants. In the latter case the runner-plant leaves were not included. Five plants were included in each group. The average values (Tables 1 and 2) are shown graphically in Figure 7 by the continuous line marked "Runners off average," representing

those from which runners were removed as formed. In this figure are shown also narrow-line graphs for the minimum value of the leaf product and for the maximum value corresponding to the two main graphs. These minimum and maximum values are not shown in Tables 1 and 2, but have been calculated from the original observational data.

It is seen that the average rate was slow till about May 13, after which it was more rapid but nearly uniform to the end of the period in the case of the runnerless plants, but only until about July 1 for the plants that were allowed to produce runner plants. After about July 15 the average graph for the latter group of plants descends slightly and then remains nearly horizontal to August 20, when these observations were discontinued. It is thus again indicated that the vigor of the parent plant was greatly increased by the removal of the runners as they appeared. In other words, the production of runners and runner plants limits the growth vigor of the parent plant through-

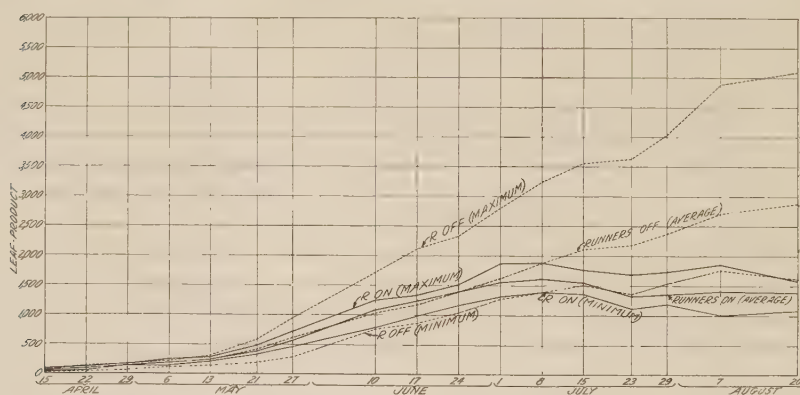


FIGURE 7.—Seasonal marches of total leaf area per plant (as indicated by values of total leaf product per plant) for plants of the Howard 17 variety of strawberry, with runners removed and with runners left and allowed to root. Five plants were included in each group; all were set out April 1, 1925

out the latter part of the season. On August 20 the average value of the total leaf product per plant of the plants without runners was nearly twice as great as that of the plants with runners.

It is to be noted, however, that the maximum deviation from the average is greater for the plants with runners removed than for the others, and that this difference becomes greater with the advance of the season.

COMPARISON OF NET MEAN DAILY INCREMENTS OF MEAN LEAF-PRODUCT VALUES FOR PLANTS WITH RUNNERS REMOVED AND WITH RUNNERS RETAINED

The seasonal fluctuations in the value of the mean daily increment of leaf production were determined in terms of the corresponding leaf-product increments for the period from April 1 to August 20, 1925. The data for these daily increments were derived from those given in Tables 1 and 2 for the plants of Howard 17. Ten plants were used before June 17, after which five plants with runners were used and five with runners removed. The results are presented in Figure 8.

For the first four intervals (April 1 to May 6) the value of the daily increment was about five, or nearly constant. For the next four intervals (May 6 to June 10) it increased until a maximum of 34 was reached for the last of these four intervals. From the interval beginning June 17 to that beginning July 15 the plants with runners removed showed steadily decreasing increment values until these values became negative (indicating net losses of leaf area) for the intervals beginning July 8 and July 15. These plants showed small positive values for the next two intervals and a small negative value for the interval beginning August 7.

The plants with runners gave positive increment values for all intervals, with much fluctuation. The values are exceptionally low for the intervals beginning July 15 and August 7.

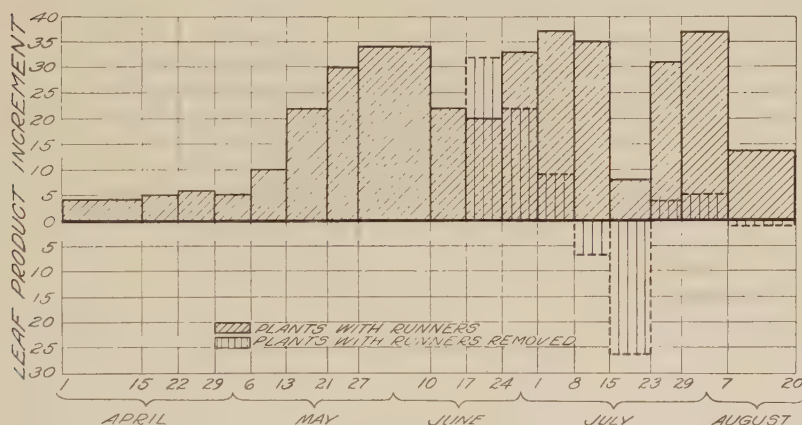


FIGURE 8.—Mean daily increments of the average value of the total leaf product per plant for each observational interval from April 1 to August 20, 1925. Before June 17, 10 plants were employed; for the rest of the period 5 plants without runners and 5 with runners were used, the two sets being treated separately

COMPARISON OF AVERAGE TOTAL LEAF-PRODUCT VALUES FOR CLONS WITH CORRESPONDING VALUES FOR THEIR MOTHER PLANTS

For the five clons of the Howard 17 variety in 1925 the seasonal march of the total leaf surface per entire clon was compared with the corresponding march of the total leaf surface per mother plant in the clon, leaf-product values being used as indicators of leaf surface. The results are shown in Figure 9. The deviation from the average is seen to be small throughout the period, becoming larger for the later dates. The graph of the averages for mother plants alone is not far from the horizontal line for 1,500, showing again that the production of runner plants soon put a stop to the regular increase in net leaf surface of mother plants that was manifest for the first three intervals considered, beginning May 13, 21, and 27. The lined area between the two average graphs represents for each interval the portion of the total leaf product per clon that was due to leaves borne by the runner plants of the clon.

By July 8 the total leaf area of the runner plants of a clon nearly equaled that of the mother plant, and by August 20 the runner-plant portion of the clonal leaf area was nearly seven times as great as the mother-plant portion.

SUMMARY

This paper reports some of the results of a series of field studies on the relations between the growth of strawberry plants and the climatic conditions throughout the growing season. As an index of growth the leaf product (which is the sum of the products of the length and breadth for all leaflets on the plant) was used, and this was found to be a better growth-index than the leaf product for the terminal or for either of the lateral leaflets or for any linear dimension.

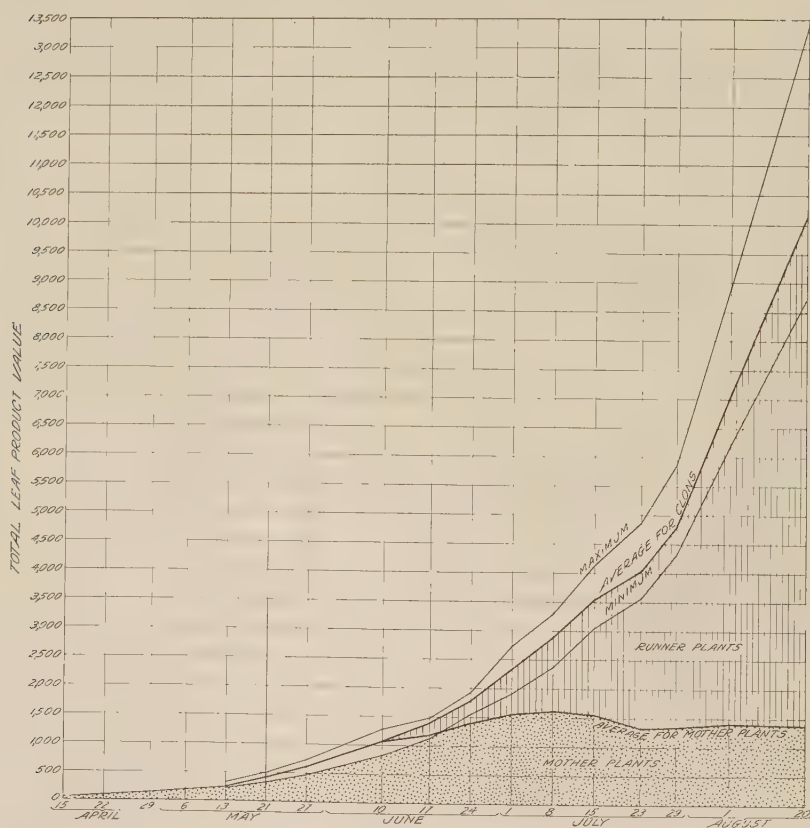


FIGURE 9.—Seasonal march of total leaf area per clon (as indicated by values of the total leaf product per clon) for five clons of Howard 17 variety, season of 1925; also the corresponding graph of the average total leaf product for the mother plant. The shaded area represents the runner-plant portion of the average total leaf product per clon at each time of observation

Measurements were taken at intervals, generally of one week, and seasonal graphs were constructed to represent the march of the leaf-product index throughout the season. Some of the climatic conditions were measured at like intervals, and graphs for these were also constructed.

A comparative study of these graphs with special reference to periods of high and low rates of leaf production leads to the conclusion that for the seasons 1925 and 1926 the limiting factor in the growth of the plants was generally temperature. In one instance, however,

low growth rates appear to have been due to drought. The temperature relations are considered in some detail, and the conclusion is reached that these data indicate high growth rates for average mean daylight air temperatures from about 68° to about 79° F., while daylight-temperature values above or below this range were generally accompanied by much lower rates of leaf production. These considerations lead to the approximation of a daylight-temperature optimum of about 73°.

It is emphasized that the results of these studies are to be regarded as valid only for the particular plants and seasonal and other environmental conditions that were involved in this work, and no generalizations are attempted.

Attention is called to the seasonal march of average mature-leaf size on spring-set plants with a seasonal maximum in June. Following the maximum, plants producing runners showed a decline in the size of their mature leaves for the remainder of the season, whereas plants with runners removed showed no such decline. This seasonal march for runner plants also showed an initial minimum, a later maximum, and a final decline. For the Howard 17 variety the average length of life of plants that unfolded between April 1 and July 8, 1925, was 56 days, with a range from 21 to 77 days. In general, the leaves died in sequence, those unfolding first being the first to die.

Plants allowed to produce runners showed a gradual increase in total leaf product until about July 8, after which this measure of leaf area decreased, but only to a slight extent for the rest of the period. By July 8 the total leaf product of the runner plants produced equaled that of the mother plants, and by August 20 it was about seven times as great.

A comparison of the seasonal march of the value of the average total leaf product per plant for 1925 for seven varieties shows that Howard 17 was the most active and Aroma the least active variety. Net leaf production by plants with runners removed was compared with that by plants with runners left on and allowed to root. The vigor of the parent plant was greatly increased by the removal of runners as they appeared, but the maximum deviation from the average was greater for these plants than for those that produced runner plants. A similar comparison was made between the mean daily increment values of total leaf product for the same plants. For plants with runners removed these values were all positive, although with much fluctuation; whereas for the plants producing runners they were generally much smaller and were actually negative (indicating a net loss) for 3 of the 17 periods.

VITA

George M(cMillan) Darrow was born February 2, 1889, at Springfield, Vermont, the son of Guy C. and Maria (McMillan) Darrow. He attended the public schools of Springfield and Chester, Vermont. In 1910 he received the degree of Bachelor of Arts from Middlebury College, specializing to some extent in botany. In 1911 he received the degree of Master of Arts from Cornell University specializing in horticulture and plant breeding. From July 1, 1911 to date he has been employed in pomological research in the United States Department of Agriculture with the exception of military service from June 1918 to August 1919. He was married in 1919 to Grace E. Chapman. From September, 1923 until June, 1927, he was a student in the Johns Hopkins University receiving the degree of Doctor of Philosophy with plant physiology as his principal subject (under Professor Burton E. Livingston). The work in the first subordinate (Genetics) under Professor Herbert S. Jennings consisted of course work together with the submission of articles on berry breeding being published. The work for the second subordinate (botany) under Professor Duncan S. Johnson consisted of course work.

In the United States Department of Agriculture he was first engaged in research on the careful handling and precooling of sweet cherries and fresh prunes in the Northwest and of citrus fruit in Florida (1911-1912). From 1912 to 1915 he made a survey of fruit varieties in West Virginia, Kentucky, Tennessee and adjacent states mapping the physiographic regions in this area. From 1916 to 1919 he made surveys of the growing of small fruits in United States. From 1920 to 1930 he has had charge of the breeding and physiological studies with small fruits at the Plant Field Station, Glenn Dale, Md., at the North Carolina Coastal Plain Station, Willard, North Carolina, and at the Oregon Agricultural Experiment Station, Corvallis, Oregon.

The principal results of his small fruit survey work are contained in fifteen farmers' bulletins on the Culture and Varieties of Small Fruits in the United States. The results of his breeding work are contained in numerous articles in the Journal of Heredity and other journals. One strawberry variety originated by him has been named and introduced, while several other berries are being propagated for introduction. The results of his physiological work are contained in the Journal of Agricultural Research and technical bulletins.

Since 1922 he has been on the Editorial Board of the American Genetic Association publishing the Journal of Heredity. For the year 1929-1930 he was vice-president of the Washington Botanical Society.

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